

THE EMBRYOLOGY OF A BRACHIOPOD,
TEREBRATULINA SEPTENTRIONALIS Couthouy.

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Plates I-X.

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I. INTRODUCTION.

1. *Historical*. — Although Brachiopoda are chiefly notable because of their great abundance in past geological periods, their relationships to other groups of animals are still so obscure as to make them objects of great interest to the general morphologist. At different times and by different investigators they have been variously regarded as allied to Mollusca, Polyzoa, Annelida, Chætognatha and Phoronis, while others have regarded them as a distinct phylum of the animal kingdom. Even at the present time there is no uniformly accepted view as to their relationships, all of the above affinities (excepting possibly the first) being maintained by different authors. Of the two morphological methods of investigating relationships, viz., Comparative Anatomy and Comparative Embryology, the former has been applied to this group of animals in a number of noteworthy cases. Not to mention the large number of older and less important works on this group, the comprehensive studies of Albany Hancock ('58) and the excellent researches of Lacaze-Duthiers ('61), which are still models of accuracy, the extended labors of Davidson ('86-'88) and most recently the series of splendid contributions by Blochmann ('92 and 1900) have made us as well acquainted with the anatomy of the brachiopods as we are with the anatomy of most other invertebrates.

The case stands far differently with the embryology of this group. But two writers have as yet attempted to deal with the entire embryology of a brachiopod, and both of these studies were made without the employment of serial sections or modern microscopical and micro-technical aids.

Neglecting the isolated observations of Fritz Müller ('60 and '61) of a free-swimming larval brachiopod, and the more extended but still very fragmentary observations of Lacaze-Duthiers ('61) on the development of *Thecidium*, the credit of having made the first study of the entire development of a brachiopod belongs to the

American naturalist, Prof. E. S. Morse ('71-'73). How thorough and complete this work was I shall have occasion to remark in the further course of this paper; but done as it was at a time before good microtomes and imbedding means were invented, and long before serial sections were thought of, it could not but leave much of the internal structure of the embryo undetermined, especially as the eggs and embryos of the form studied (*Terebratulina septentrionalis*) are quite small and opaque. Nevertheless Morse's work stands to-day as one of the two most important works on the embryology of the brachiopods. The other work referred to is the later but more detailed and comparative "Observations on the Development of Brachiopods," by the great Russian zoölogist, Alexander Kowalevsky (1874). Kowalevsky's work, which was published in Russian, remained practically unknown to those not acquainted with that tongue until 1883, when Oehlert and Deniker published an excellent abstract of it. In this work Kowalevsky describes his observations on the development of four species—*Argiope* (*Cistella*) *neapolitana*, *Thecidium mediterraneum*, *Terebratula minor* and *Terebratulina caput-serpentis*; only a few observations were made on the development of the two last-mentioned species, but his work on *Cistella* and *Thecidium* was detailed in character and nearly complete so far as the stages of development are concerned. Although Kowalevsky employed isolated sections to a limited extent in his work and also shows certain details of internal structure in many figures of entire embryos, yet his work of necessity left many important problems of structure unsolved.

In 1879 Prof. W. K. Brooks discovered the free-swimming larvæ of *Lingula* (*Glottidia*) *pyramidata* and described in detail the structure and further development of these larvæ up to the adult condition. This work, although dealing only with the larval stages and metamorphosis, is still the most complete extant on the development of the Ecardines, the most primitive group of the brachiopods. With characteristic insight Brooks has used his many important discoveries on the later development of *Glottidia* in an extremely valuable discussion of the systematic position of the brachiopods.

The small portion of Shipley's (1883) paper on *Argiope* (*Cistella*) which treats of the development of that form adds little to the much more extensive work of Kowalevsky on that animal. His principal contribution consists in his determination of the fact that

the so-called "segments" of the larva are not true segments, as Kowalevsky supposed, but are mere folds in the body wall.

The papers by Beecher ('91, '92, '93) on the development of brachiopods deal almost entirely with the developmental changes which occur in the shell and not with the general embryology. Beecher has proposed a very interesting and important classification of the brachiopods based on the developmental characters of the shell; since however the present work deals only with the early embryology, we need not further consider Beecher's work here.

2. *Material*.—For the material which has formed the basis of this study I desire at the outset to express my profound obligations to my friend Dr. Edward G. Gardiner, of Wood's Holl, Mass. Dr. Gardiner had collected the material (which consists of about thirty different stages in the early embryology of *Terebratulina septentrionalis*, forming a fairly complete series from the unsegmented egg up to the beginning of the metamorphosis) at Eastport, Me., during the early summer of 1894. For various reasons he was prevented from making an immediate study of this material, and when in the summer of 1898 in conversation with him I expressed my desire to study the cell lineage of a brachiopod, he graciously offered me the material which he had collected with the request that I should use it in any way I might see fit. I soon found that it would be impossible to work out the cell lineage, not only because of a lack of sufficient number of cleavage stages, but also and chiefly because of the great difficulties which the material itself offered; the eggs were quite opaque and, except in a few cases, it was impossible to render the nuclei visible in preparations of the entire egg; the cleavage was almost entirely equal and I was unable to find any constant landmarks which might be used in orientation, and finally the cleavage was found to be more or less irregular and inconstant. I was compelled therefore to abandon the plan to study the cell lineage of *Terebratulina* and the material was laid aside, until a few months ago I found opportunity to again take up this subject with the view of working out the early development of this interesting animal in as great detail as the material would allow.

3. *Methods*.—All the material was, I believe, preserved in Perenyi's fluid, and while the general form and size of the embryo as a whole, and also of its constituent cells and nuclei, has been faithfully preserved, every trace of the cilia, which according to Morse ('71-'73) cover the surface and line the alimentary tract and

body cavity, has entirely disappeared. The method of fixation, together with the long residence of the material in alcohol, rendered it difficult to stain. The picro-hæmatoxylin, which I have used with such good results in other cases, was of little value here, and I have found that in the preparation of entire eggs or embryos the most useful stain is borax carmine, while in the preparation of sections iron hæmatoxylin has given the best results. Both entire preparations and serial sections were mounted in balsam and studied and drawn under an immersion lens (Zeiss. Apochromat. 3 mm., Comp. Occ. 4).

Perhaps I may be pardoned a word in defense of the rather large use of surface views and optical sections which I have made in this paper. This has not been due to the fact that I have made few serial sections, for I have made and studied serial sections of many hundreds of embryos, but because with material which is at all favorable the orientation of the embryo and the interrelation of its various parts can be more safely and satisfactorily determined from the study of whole embryos than by means of serial sections; and this is especially true where it is possible to use an immersion lens in the study of entire preparations. Further, more points of structure can be shown in a single figure of this kind than in dozens of figures of serial sections. Of course, serial sections must always be used in connection with the study of entire preparations, and in the present paper all the details of internal structure which are shown in the surface views and optical sections have been confirmed again and again by serial sections. Any one accustomed to the study of both entire preparations and serial sections knows that few things are more deceptive than the latter when not checked by a study of the former, while the publication of whole series of sections contributes more to the pride of the author and the income of the illustrator than to the edification of the reader.

II. THE EGG AND ITS CLEAVAGE.

Morse ('71) has described the method of egg laying, and has called attention to the fact that the mature eggs are usually kidney-shaped, though they vary considerably in shape and size. None of the unsegmented eggs which I have examined are kidney-shaped; they are slightly elliptical, being about $160\ \mu$ in the longest diameter and $144\ \mu$ in the shortest. This elongation of the egg in one

axis is probably the precursor of the first cleavage at right angles to that axis. Morse ('73) also mentions the presence of a "distinct granular membrane, the ovishell, which is formed while the eggs are still in the perivisceral cavity." I have found this membrane in all early stages (Figs. 1-10), though I have not been able to recognize it after about the twenty-cell stage. From the fact that it lies close to the periphery of each cell, following all of its individual curvatures (Figs. 2-10), I am convinced that it is not a distinct membrane but only a peripheral layer of clear protoplasm (ectoplasmic layer of Harmer). There is no protoplasmic area in the egg distinct from the yolk, though there is a slight aggregation of protoplasm around the nuclei, but the entire egg is densely packed with small yolk granules which render it opaque.

I have not attempted to study the nuclear phenomena of the maturation and cleavage since the material is very unfavorable for such work. Two polar bodies are formed, the first of which soon after divides (Figs. 1 and 2). These polar bodies do not remain attached to the egg after the sixteen-cell stage, and in some eggs they appear to pass into the cleavage cavity, though in such cases it is difficult to distinguish between polar bodies and small spherules which are cut off from the inner ends of the cleavage cells, and which contain protoplasm and yolk but no nuclei (Figs. 11 and 37). At the stage when the gastrulation begins these spherules are found in considerable numbers in the cleavage cavity (Fig. 37); they disappear in later stages. Similar spherules have been observed by Caldwell ('85) in *Phoronis*.¹

The first cleavage is meridional and divides the egg into two slightly unequal blastomeres (Fig. 2); the second cleavage is also approximately meridional and divides each of the blastomeres equally; as a result of this cleavage four blastomeres are formed, two of which are somewhat smaller than the other two (Fig. 4). A polar furrow is present (Figs. 4 and 7) which, taken in connection with the overlapping of certain cells (Fig. 3), indicates that in some eggs at least the cleavage is of a spiral type. The third cleavage is equatorial and leads to the formation of eight blastomeres, all of which are nearly equal in size (Figs. 5, 6, 7); in some eggs the four cells at the animal pole lie just above those at the vegetal pole (Fig. 6); in others they have rotated through various

¹ Quite recently Ideka (1901) has fully described these spherules in *Phoronis*; he calls them *plasmic corpuscles*.

angles (Figs. 5 and 7). In the eight-cell stage a considerable cleavage cavity appears with openings at the animal and vegetal poles (Figs. 6 and 7).

The cleavage forms just described and represented in Figs. 1-7 are among the most regular ones observed; others are irregular and unequal from the first. One of the most common variations is produced by very unequal divisions, the chief mass of the egg seeming to bud off small cells, usually at the animal pole (Fig. 8). Later stages in which one or two of the blastomeres are much larger than the others, and in which the cleavage cavity is smaller than usual, are not infrequently found. Such eggs appear to give rise to normal blastulæ, in which all the cells are of equal size, by the more rapid division of these larger blastomeres.

The eight-cell stage gives rise to the sixteen-cell stage by the meridional division of each of its blastomeres. Fig. 7 shows each blastomere of the eight-cell stage indented at its periphery, preparatory to this division, which occurs simultaneously in all of the cells. The sixteen cells shown in Fig. 9 and in optical section in Fig. 10 are all of approximately the same size. Except for the occasional presence of the polar bodies at this stage it would be impossible to distinguish the animal from the vegetal pole. The cleavage cavity is now larger and it no longer opens widely to the exterior.

In subsequent cleavage stages division does not take place simultaneously in all of the cells; this is shown, for example, by Fig. 11, in which twenty cells are present, some of which are considerably larger than the others. In the eggs represented in Fig. 12 about forty-eight cells are present and some of these are larger than others, indicating that with them division has been delayed. The egg shown in Fig. 12 has been flattened by the cover glass, so that its apparent diameter is greater than normal; at the same time the blastomeres are separated from one another in an abnormal manner. At all stages the blastomeres are but loosely joined together and they break apart at the slightest pressure. In the later development I have found many embryos which are about one-half or one-quarter the size of the normal embryo, and it seems likely that such embryos have developed from isolated blastomeres of the two- or four-cell stage.

After this brief description of the cleavage, I think it will be quite apparent to everyone that it would be extremely difficult, if

not quite impossible, to work out the cell lineage of *Terebratulina*, even with an abundance of most favorably preserved material. With the material at my disposal such work was wholly out of the question. In the blastula, even at the time when gastrulation begins, one is struck by the great uniformity in size and quality of all the cells. I have found it quite impossible to distinguish any difference between the cells which invaginate and those which do not until after the gastrulation is well advanced.

III. GASTRULATION AND FORMATION OF BODY LAYERS AND CAVITIES.

Gastrulation occurs by typical invagination, and at the time when the infolding begins there is no difference in the cells at the two poles (Figs. 13 and 37). The infolding continues until the inner layer comes into contact with the outer one and the blastocoel is entirely occluded (Fig. 14 *et seq.*). During this process there is a decided change in the character of the cells of the inner layer; they become very much shorter and henceforth are cuboid or rounded in shape; the cells of the outer layer remain columnar in shape and are very long, so that the ectoderm is quite thick. Large deeply staining granules are found at the free ends of all the cells, both those which are invaginated and those which are not, and in the invaginated cells these granules are so dense that they frequently obscure the nuclei and cell boundaries. In the ectoderm these granules lie on the outer side of the nuclei (Fig. 37 *et seq. Pg.*), while the inner ends of the cells are left free from granules and nuclei and hence are very clear. I suggest that these granules may be associated with the cilia, which in life cover the embryo and line the enteron and coelom (see Morse, '73).

Almost as soon as the inner layer comes into contact with the outer one—*i. e.*, when the infolding is complete—the innermost portion of the archenteron becomes slightly constricted from that portion lying nearer the blastopore. This constriction is deepest anteriorly, least marked posteriorly, while it is about equal on the left and right sides of the archenteron (Figs. 14, 15, 16, 38). On the anterior side this constriction develops into a partition wall, which grows downward and backward into the archenteron, shutting off the enteron above from the enterocoel below (Figs. 16, 20, 42*a* and 42*b*). So far as I am able to determine this partition wall

is always but one cell thick (Figs. 40-42), though in the earlier stages of its development it represents a fold in the wall of the archenteron (Figs. 42*a*-42*b*). The backward growth of this partition wall continues until the enteron is entirely separated from the enterocœl save for a narrow slit-like communication at the posterior end (Figs. 20, 24).

While the enteron is thus being separated from the enterocœl the blastopore is gradually closing and the whole embryo is becoming flattened in a dorso-ventral direction and elongated antero-posteriorly. The blastopore is at first a circular opening; it then becomes narrowed from side to side and apparently elongated antero-posteriorly (Figs. 17-21). The blastopore groove thus formed is shallow posteriorly and deepest at its anterior end where it opens into the enterocœl and enteron (Fig. 17). This groove continues to grow narrower and to be filled up at its posterior end until it becomes a mere slit, opening by a small pore near its anterior end into the enterocœl (Figs. 21, 22). Finally this pore also closes (Fig. 24) and the enterocœl and enteron are completely shut off from the exterior, though still communicating with each other by a narrow opening in the region posterior to where the blastopore closed (Figs. 24 and 46, 47). The blastopore groove persists for some time after the pore has closed but ultimately disappears, though a depression is left at the anterior end of this groove which becomes a part of the anterior mantle furrow; it is probable that at this very point the œsophageal invagination occurs at a stage after the fixation of the larva (see p. 56).

In stages in which the blastopore is still circular the enterocœl is but little larger than the enteron (Figs. 14 and 38). In looking at an entire egg of this stage from the oral side one sees two cavities of about the same diameter, one above the other, which communicate with each other by a wide opening; the cavity nearest the blastopore is the enterocœl, the one nearest the aboral side the enteron. In an older stage (Fig. 17) in which the blastopore has begun to narrow one still sees that these two cavities are of nearly the same diameter. As the enteron becomes separated from the enterocœl, however, the latter becomes much more extensive than the former, and an oral view of an embryo at this stage shows the enterocœl lying on the oral side of the enteron and entirely surrounding it except on the aboral side (Fig. 21, also optical sections, Figs. 19 and 20). This rapid enlargement of the enterocœl

is due in large part to the change in shape of the embryo, which becomes flattened in a dorso-ventral direction and enlarged in its other axes. Associated with the growth of the enterocœl is an important change in the character of its bounding cells; at first they form a quite regular, cuboid or columnar epithelium (Figs. 14-16 and 40-42*a*), but as the enterocœl increases in size the epithelium becomes less regular, particularly at the anterior end, and here many mesenchyme cells come to lie in the cavity of the enterocœl (Figs. 20, 21, 42*b*, 43). Later such mesenchyme cells are found generally throughout most of the cœlom. The cells bounding the enteron remain cuboid or columnar throughout the development.

With the flattening of the embryo and the closure of the blastopore, the ventral wall of the enteron is brought into contact with the ectoderm at the place where the blastopore closes (Figs. 24 and 44-47), and consequently the enterocœl is here divided into right and left cavities, which however still communicate with each other at the anterior end and open into the enteron posteriorly (consult Figs. 43-47 which are transverse sections of an embryo of the stage shown in Fig. 24, Fig. 43 being the most anterior section drawn and Fig. 47 the most posterior). Very soon after this stage the communication between the enteron and the enterocœl is completely cut off and the definitive cœlom is thus formed, consisting of two sacs, still opening into each other anteriorly and posteriorly but separated throughout the middle region of the embryo (consult Figs. 48-52 which are cross sections, in order from the anterior to the posterior region, of an embryo of about the stage shown in Fig. 28).

The gastrulation and formation of body cavities in brachiopods has been observed heretofore only by Kowalevsky. A comparison of the method of gastrulation and cœlom formation in *Terebratulina* with Kowalevsky's observations on *Cistella* and other brachiopods reveals many resemblances and some interesting differences. Kowalevsky found that the gastrula was formed by invagination in *Cistella*, *Terebratula* and probably *Terebratulina*; by delamination or ingression in *Thecidium*. In all cases, however, he describes the cœlom as arising as two lateral pouches from the archenteron in the same manner as in *Sagitta*, viz., by the folding into the archenteron of two lateral partitions. In this way the archenteron is divided into three portions, a median one which becomes the

enteron and two lateral ones which form the cœlom. It is difficult to determine from Kowalevsky's figures from which portion of the archenteron these lateral partitions arise, but there can be no doubt that they are regarded as *folds* of the archenteric wall (see his Fig. 6), nor that they divide the archenteron into three cavities, the enteron and two cœlom sacs. In both of these respects *Cistella* is very unlike *Terebratulina*; in the latter the archenteron is first divided into two cavities and not three (the enterocœl is for a long time unpaired), and the single partition wall by which this division is brought about consists of a single layer of cells and not a plication of the archenteric wall (though in its earliest stages this partition wall probably represents such a plication, Fig. 42a). The former of these differences is perhaps not so great as would at first thought appear, being principally due to the fact that in *Terebratulina* the enteron occupies but a small part of the archenteron, and hence the partition wall which separates it from the enterocœl leaves the latter a large unpaired cavity, whereas in *Cistella* the division of the archenteron is more nearly equal and when completed separates two lateral enterocœl pouches from the median enteron. But one cannot overlook the fact that according to Kowalevsky two partition walls are formed in *Cistella*, whereas but a single one is found in *Terebratulina*. Moreover these partitions are lateral in position according to Kowalevsky, whereas in *Terebratulina* the single partition grows out from the anterior wall and merely curves around on to the lateral walls of the archenteron (Fig. 16). The difference in the structure of this partition in *Cistella* and *Terebratulina* is also important; in the former it consists of a double layer of cells, in the latter of a single layer; in *Cistella* the wall of the enterocœl sacs lying next to the enteron becomes the splanchnic layer of the mesoblast, in *Terebratulina* the splanchnic mesoblast is derived from mesenchyme cells. Before attempting to explain these important differences between *Cistella* and *Terebratulina* in the formation of the cœlom it would be well to know that they actually exist, and it seems highly desirable that the embryology of *Cistella* should be reinvestigated with the aid of modern histological methods.

The differences between *Terebratulina* and *Sagitta* in the mode of forming the cœlom are of interest since they remove one important argument for the supposed relationship between Brachiopoda and Chætognatha.

IV. ORIENTATION OF THE EMBRYO AND ESTABLISHMENT OF DEFINITIVE AXES.

It is well known that previous investigators of the embryology of the brachiopods have found the proper orientation of the embryo one of their most perplexing problems. The complete closure of the blastopore at a relatively early stage and before many landmarks have appeared by which its position relative to definitive organs could be determined, as well as the fact that both the oral and aboral sides of the embryo are very similar, has been chiefly responsible for this uncertainty of orientation. However if one studies carefully whole embryos of the critical stage when the last remnant of the blastopore is disappearing, the proper orientation of the embryo of a brachiopod is no more difficult than is that of any other animal.

In the stage shown in Figs. 23 and 24 the antero-posterior axis of the embryo is well defined, while the remnants of the blastopore are still present. The enlarged end of the embryo (to the right in Fig. 24) is anterior and gives rise to the head, while the posterior end (to the left in the figure) is narrowed and gives rise to the peduncle. The point where the blastopore closed (Fig. 24, *Br*) lies near the middle of the ventral side, while the blastopore groove runs backward almost to the posterior end of the embryo. Directly opposite the blastopore is a groove which runs transversely across the dorsal side of the embryo; this is the dorsal mantle groove, and the prominent ridge anterior to it is the dorsal mantle fold (Fig. 24, *Md*). If now Fig. 24 be compared with Figs. 20 and 16 it will be seen that the blastopore occupies the ventral-posterior region of the embryo, and that the anterior pole of the embryo is rounded while the posterior pole is pointed, the embryo being flattened on its postero-dorsal side. The prominent ridge opposite the blastopore in Figs. 16 and 20 corresponds with the dorsal mantle fold in Fig. 24. A comparison of these three figures further shows that the axis connecting the middle of the blastopore with the apex of the gastrula invagination (*e. g.*, *E* in Fig. 14) is ultimately bent on itself through an angle of more than 90°. It is difficult to say whether this bending of the gastrula axis is chiefly due to the forward shifting of the blastopore on the ventral side or to the forward shifting of the apex of the gastrula invagination, since there are no points in the embryo which may be

considered as fixed in position. It is highly probable however that both movements occur and that both the apical pole and the blastopore pole are shifted forwards, while the middle of the gastrula axis is shifted backwards, the gastrula axis thus being doubled on itself exactly as is the case in Turbellaria, Annelida and Mollusca. Since the polar bodies have long since disappeared it is impossible to locate exactly on the embryo the point which corresponds to the animal pole of the egg. It is probable, however, that this point lies on the ectoderm directly opposite the apex of the gastrula invagination, and therefore anterior to the ridge which develops into the dorsal mantle fold. In the forward shifting of the apex of the gastrula invagination it is highly probable that this point is also shifted forward and continues to lie opposite the apex of the enteron. If this be true the animal pole of the egg coincides very nearly with the point where the line from *Ce* in Figs. 20 and 24 touches the ectoderm.

The bending of the gastrula axis which has just been described shows that *Terebratulina*, like most bilateral animals, belongs to the group designated by Hatschek ('88) Heteraxonia, and by Goette ('82) Hypogastric forms. Goette has divided bilateral animals into two groups: (1) the pleurogastric, in which the chief axis of the egg becomes the chief axis of the larva or adult, as in *Sagitta* and the echinoderms, and (2) the hypogastric, in which one of the "cross axes" of the egg becomes the chief axis of the larva or adult, as in worms, mollusks and arthropods. There can be no doubt that *Terebratulina* should be classed among the hypogastric forms, and if it be true, which however seems questionable, that *Sagitta* and the echinoderms belong to the pleurogastric type, it shows a very important difference between the embryo of the brachiopod and of the chaetognath.

V. DEVELOPMENT AND ORGANIZATION OF THE LARVA.

There is of course no natural line of demarcation between the embryo and the larva, but for the sake of convenience we shall designate those stages which precede the closure of the blastopore as embryonic, while those which extend from the closure of the blastopore to the end of the free-swimming life we shall call larval stages.

The flattening of the embryo in the dorso-ventral axis and its

elongation antero-posteriorly have already been described. At the same time the embryo becomes wider at its anterior end and narrower posteriorly. The dorsal mantle groove and fold appear and the fold extends over on to the ventral side of the larva as a slight swelling on each side of the midline (Figs. 25 and 26). These are the halves of the ventral mantle fold and at first they are separated in the mid-ventral line by the blastopore groove (Fig. 26, *Bf*), while the blastopore remnant (*Br*) lies at the anterior end of this groove. Very soon after this stage the halves of the ventral mantle fold fuse with each other, thus obliterating the last trace of the blastopore groove, while a deep notch on the anterior side of the ventral mantle fold (Fig. 29, *O*) represents the place at which the blastopore remnant was last seen.

1. *The Mantle Fold* is at this stage a ring-like prominence which extends all the way around the larva (Figs. 29, 30, 31). This ring passes obliquely around the larva, being nearer the anterior end on the dorsal side and nearer the posterior on the ventral side (Fig. 31). Two mantle furrows are now plainly distinguishable, one in front of and the other behind the mantle fold. The anterior furrow is deepest on the ventral side, while the posterior one is deepest on the dorsal side (Figs. 29-31). With the appearance of the mantle, bounded anteriorly and posteriorly by these constrictions, the mantle furrows, three regions may be recognized in the larva, viz., the cephalic region, in front of the anterior mantle furrow, the mantle, between the anterior and posterior furrows, and the peduncular region, behind the posterior mantle furrow.

These constrictions, which I have called the anterior and posterior mantle furrows, continue to grow deeper but at no time do they form true septa which divide the coelom. The regions which they separate are not, therefore, segments, as Kowalevsky supposed. The larva is at this, and all other stages which I have studied, unsegmented, and the appearance of segmentation is due merely to the formation of the mantle from the middle region of the body.

The mantle becomes a very prominent ring around the body, and then its free edge is turned backwards until it surrounds the peduncular regions on all sides (Figs. 32-36). A space is left between the mantle and the peduncle which is the peduncular chamber (Figs. 34 and 36, *PC*). This chamber is a little deeper and wider on the dorsal than on the ventral side, which is due to the fact

that the posterior mantle furrow is deeper and is farther forward on the dorsal than on the ventral side (Fig. 31, *Fp*).

When the mantle has reached the limit of its backward growth it entirely covers the peduncle, the extremity of which nearly fills the circular opening of the mantle chamber (Figs. 34 and 36). This is the oldest stage which I have had opportunity to study. Morse ('71) has observed in detail the transformation of this larva into the adult. He figures a great many stages showing the manner in which the mantle is turned forward over the cephalic region, its free edge being directed forward and its originally internal surface becoming external. This happens after the larva has become fixed by the tip of its peduncle, and it is evident from Morse's figures and descriptions that the stage shown in my Figs. 34-36 is one of the last stages in the free-swimming life.

2. *The Cephalic Region* lies in front of the anterior mantle fold and is nearly hemispherical in shape, being however somewhat variable in form (consult Figs. 32-36), which is probably due to the fact that it is extremely contractile, as Morse has observed. At its anterior end and slightly toward the dorsal side is a shallow depression, the apical sense plate, which bears a tuft of long cilia in life (see Morse). The enlarged end of the enteron as well as a portion of the mesoderm and coelom extend into the cephalic region.

3. *The Peduncular Region* is cylindrical in shape and is contracted near its posterior end. This contraction is due to the fact that the coelom and mesoderm terminate abruptly some distance in front of the end of the peduncle (Figs. 34 and 36), and it is certainly not to be taken as constituting a fourth region of the larva, as Shipley ('82) suggests in the case of *Cistella*. The endoderm is continued as a solid cord of cells nearly to the end of the peduncle.

4. *The Ectoderm* covering the larva is unusually thick, though consisting of but a single layer of cells; these cells are however extremely long. Their inner ends are clear and free from nuclei and granules, so that on first examination a clear zone seems to separate the outer from the inner layer (Figs. 38 *et seq.*). Only on the anterior side of the mantle fold does the ectoderm become cuboid or squamous, while over the cephalic and peduncular regions it is particularly thick.

5. *Setæ Sacs*.—High columnar cells line the peduncular chamber,

and at four places (two median and two lateral) on the dorsal side of the mantle the epithelium is invaginated to form the setæ sacs (Figs. 34, 36, 56-64, *SS*). No traces of setæ are preserved in the material which I have examined, but there can be no doubt from Morse's ('73) account that these invaginations give rise to the lateral and median bundles of temporary setæ.

6. *Sense Plates and Ganglia*.—A little toward the dorsal side of the apex of the cephalic lobe is a depression in the ectoderm, and in this region the cells are deeply pigmented, especially at their free borders. This is the apical sense plate (*Scheitelplatte*) (Figs. 26, 28, 29, 31, 32, 34, 35, 36, 56, 57, 58, *CG*), and in life bears a tuft of long cilia (see Morse, '73), though no trace of these is left in the material which I have examined. At the base of the cells of this sense plate ganglion cells are cut off from the epithelial cells, but continue to lie in the ectoderm (Figs. 28, 36, 56, 57). These ganglion cells are small and I have been unable to observe their further development, but there seems no reason to doubt that they represent the cerebral ganglion.

A similar sense plate and ganglion is formed on the midventral line immediately posterior to the place where the blastopore remnant closed and in the region where the blastopore lips fused along the mid-line (Figs. 29, 31, 35, 58, 61, 62, *SG*). This is the ventral sense plate, and the cells of this plate are pigmented as are those of the apical plate; I think it probable that they bear a tuft of long cilia in life, although no one has observed this feature as yet. As in the case of the apical plate, ganglion cells are cut off from the basal ends of the epithelium of the ventral plate, and here again there seems every reason to believe that these ganglion cells become the subœsophageal ganglion. The œsophagus has not formed in the oldest larva which I have been able to study, but a slight invagination of the ectoderm immediately anterior to the ventral sense plate probably represents the earliest step in the formation of the œsophagus (Fig. 58, *O*). Heretofore no observations have been made on the early development of the nervous system. Neither Morse nor Kowalevsky observed any stages in the formation of the nervous system. Shipley has observed in the head region of *Cistella* a small clump of cells without granules, which he suggests may be a nerve ganglion; his Fig. 35 shows however that it lies entirely within the mesoderm, and it cannot therefore be a ganglion. Brooks has described in detail the nervous system of the larva of

Glottidia, but this system is already well formed in the earliest larva which he observed.

7. *Enteron*.—The cavity of the enteron is flask-shaped, the enlarged end lying in the cephalic region while the pointed extremity extends into the peduncle. In early larval stages the transverse diameter of the enteron is greater than its dorso-ventral diameter (Figs. 25 and 44-50); in later stages it becomes circular in cross section (Figs. 53-55), while in still later stages it becomes compressed laterally so that its greater diameter is in a dorso-ventral direction (Figs. 33, 35, 56-60). In the oldest stages which I have observed a diverticulum from the anterior end of the enteron grows out toward the ventral side, and at the same time an invagination of the ectoderm appears in the anterior mantle furrow, at the very point where the blastopore remnant disappeared, and grows in toward this diverticulum (Figs. 35 and 58). I presume that this is the first step in the formation of the œsophagus. During the whole of the larval period the enteron has no opening to the exterior. According to Morse ('73) the mouth is formed late in the metamorphosis, and while he does not describe the place or manner of its formation his Fig. 90 shows it at the anterior extremity of the young brachiopod. Kowalevsky ('74) also has described and figured what he considers to be the formation of the œsophagus at the anterior end of the cephalic lobe. From what I have observed I feel confident that the mouth is first formed on the ventral side, in the region of the anterior mantle furrow, and if it is later found at the anterior end of the young brachiopod, its change in position must have been brought about by secondary changes. Kowalevsky expresses some doubts as to whether the invagination observed by him at the anterior end of the cephalic lobe is really the œsophagus, and from its location I would suggest that it is the apical sense plate and cerebral ganglion rather than the œsophagus. My observation as to the location of the stomodæal invagination thus confirms Heider's ('93) theoretical suggestion and brings the brachiopod larva into close relationship with the trochophore.

The cells bounding the lumen of the enteron are cuboid in early stages and columnar in later ones (compare Figs. 43-50 with Figs. 56-60). These cells, enclosing a minute lumen, extend through the entire peduncular region (Figs. 36, 57, 58, 61-64).

From its earliest formation the enteron is in contact on its dorsal

side with the ectoderm, while laterally and on its ventral side it is bounded by mesoderm (Figs. 43-52, 58 and 61-63).

8. *Cœlom*.—For a long time after the division of the cœlom into right and left cavities by the flattening of the embryo and the closure of the blastopore these sacs communicate with each other both anteriorly and posteriorly (Figs. 43-47, 48-52, 53-55). In still later stages these communications are closed by the practical elimination of the cœlom in the cephalic and peduncular regions through the proliferation of mesenchyme cells (Figs. 56-63). The cœlom sacs, which are at first of nearly the same size both anteriorly and posteriorly (Fig. 25), become much constricted in the peduncular region while they still remain large in the head and mantle regions (Fig. 26). In the latter region they then become lobulated, often showing a trefoil condition (Figs. 27, 28), and with the further development of the dorsal and ventral mantle folds a lobe of the cœlom is sent into each of these folds (Figs. 29-33). At the same time the cœlom in the cephalic and peduncular regions grows smaller, while that in the mantle grows larger. Finally almost the entire cœlom is contained in the mantle, the portion in the head and peduncle being very small (Figs. 36 and 56-63). The posterior limits of the peduncular cœlom is marked by a narrowing of the peduncle, which probably represents the fourth "segment" of Shipley. The cœlom however is never segmented though it may be constricted in certain places. The constrictions shown in Figs. 27-31 are quite constant in position and are connected with the extension of the cœlom into the mantle lobes, but they never coincide in position with the superficial constrictions of the body (mantle furrows). In a few abnormal larvæ of the stage shown in Fig. 25 I have found each cœlom sac partially divided by mesenchyme cells into three cavities. That these divisions, however, have no real importance is shown by the fact that their number differs in different larvæ and is sometimes different on opposite sides of the same larva.

In the early larval stages the enteron is in close contact with the ectoderm on the dorsal side, while a collection of mesoderm cells on the ventral side of the enteron separates the two cœlom sacs and may be considered the rudiment of a ventral mesentery (Figs. 49, 50).

In later stages the cœlom is almost entirely obliterated, except in the mantle, and consequently the enteron is surrounded by

a dense mass of mesoderm cells, except on the dorsal side, where it is still in contact with the ectoderm (Figs. 56-64). At this stage therefore there can be no mesenteries since there is practically no coelom.

In early stages of larval life the mesoderm cells are mesenchymatous in the anterior region of the body and epithelial in the posterior regions (*cf.* Figs. 43-46). In the later stages the mesoderm cells of the posterior regions become more mesenchyme-like (Figs. 48-52 and 53-55), while in still later stages they become densely packed and pigmented and it is impossible to distinguish their cell boundaries (Figs. 56-64).

VI. GENERAL CONSIDERATIONS AND CONCLUSIONS.

Although I am not one of those who expect to find phylogeny "writ large" in ontogeny, yet it may be worth while to point out the bearings of the development of *Terebratulina* on the supposed relationships of brachiopods. Since my own studies cover only the embryonic and larval periods, I shall of course limit to those periods the comparison of *Terebratulina* with other forms. Within these periods we may compare (1) the cleavage, (2) mesoderm and coelom formation, (3) orientation of embryo and larva, (4) the general morphology of the larva.

1. *The Cleavage*.—As has been said already, there is no evidence that the cleavage of *Terebratulina* resembles that of mollusks or annelids. It is now known that in a great many annelids and leeches and in all groups of mollusks except the cephalopods the cleavage is of a certain determinate or morphogenetic (Child, 1900) type. The principal characteristics of this type of cleavage are that the ectoderm is segregated in three quartettes of cells, that the greater part of the mesoderm appears in one cell (4d) of the fourth quartette, and that the remaining cells of the fourth quartette together with the basal cells (macromeres) constitute the endoderm, and finally that the elongation of the embryo takes place by the teleoblastic cleavage of certain cells in the ectoderm and mesoderm (first and second somatoblasts, 2d and 4d) and possibly also in the endoderm (endodermic derivations of 4d). In addition to these general characteristics of the cleavage of annelids and mollusks there are other characteristics less general in application, such as the derivation of the prototroch, the stomodæum, the cerebral

ganglia, etc., from certain cells of the ectoderm. Wilson ('99) has shown that many of the general characteristics mentioned above are applicable also to the cleavage of the Turbellaria.

With regard to some of these general characteristics it is impossible at present either to affirm or deny their presence in *Terebratulina*. For example, owing to the difficulty of identifying individual cells I cannot say whether or not the ectoderm is segregated in three quartettes. In fact I am wholly unable to recognize quartettes at all after the eight-cell stage. It is certain, however, that the mesoderm is not formed by teleoblastic growth from a single cell and that the embryo does not grow in length by the teleoblastic cleavage of two somablasts. Furthermore the cleavage of *Terebratulina* shows no resemblance to any type of determinate or morphogenetic cleavage which has yet been described, whether among annelids, mollusks, turbellarians, nematodes or ascidians. On the other hand it does resemble in some respects the indeterminate cleavage of echinoderms, Phoronis and ectoproctous Bryozoa.

2. *Mesoderm and Cœlom*.—The gastrulation occurs by typical invagination; however, this method of gastrulation is found in almost every great group of animals, and therefore no phylogenetic significance can be attributed to it. In the formation of the cœlom however the case is somewhat different. The method of mesoderm and cœlom formation in *Terebratulina* is totally unlike that which is found in annelids, mollusks, platyhelminths, nematodes and arthropods, while it shows certain resemblances to chætognaths and echinoderms. A more detailed comparison shows however that even these resemblances are not very close.

In echinoderms the enterocœl is formed at the inner end of the archenteron, while the enteron arises from that portion of the archenteron nearest the blastopore; in brachiopods the enteron is formed from the inner end of the archenteron, while the enterocœl arises from that part of the archenteron which in echinoderms gives rise to the enteron. It is evident therefore that no real resemblance exists between echinoderms and brachiopods in this respect.

In chætognaths the method of cœlom formation is more like that in brachiopods—in fact Kowalevsky supposed that the two were identical—and yet there are important differences here also. In *Sagitta*, according to both Kowalevsky ('71) and Hertwig ('80), two bilateral folds of the archenteric wall grow into the archen-

teron from its apex, thus dividing the cavity into a median one, the enteron and two lateral ones, the enterocœls. The stomodæum is said to open into the apical end of the enteron, directly opposite the blastopore, which has however closed at an earlier period. In *Terebratulina*, on the other hand, the enteron is separated from the single enterocœl by one partition which grows out from the anterior wall of the archenteron and divides the latter into a dorsal cavity, the enteron, and a ventral one, the enterocœl; only later, by the closure of the blastopore and the flattening of the embryo, does the enterocœl become divided through its middle region into right and left cavities, which, however, continue for some time to communicate with each other both anteriorly and posteriorly. Moreover the stomodæum in *Terebratulina* is formed in the position of the former blastopore and not on the opposite side of the embryo. Therefore, although there are certain general resemblances between the two, I cannot regard the cœlom formation in chætognaths and brachiopods as being more than analogous processes, and as such devoid of phylogenetic significance.

In *Phoronis*, according to Caldwell ('85), two pairs of cœlomic cavities are formed by a modified type of enterocœl formation, which however bears no resemblance to that in *Terebratulina*. The anterior one of these cavities gives rise to the cavities of the epistome and lophophore, the posterior one to the chief body cavity.

Masterman's (1900) work on the development of *Phoronis* furnishes the most complete account of the early development of this interesting form which has yet been given.¹ In an earlier work ('97) he found that there were three separate and distinct cœlomic cavities in the larva, a preoral or epistomal cavity, a collar or lophophoral cavity and a trunk cavity. In his later paper he describes the origin of these cavities; the first of these arises as a median outgrowth from the anterior side of the archenteron, the other two arise as paired masses of solid mesoderm cells in which cavities appear later. In the matter of the formation of the anterior or procœlomic cavity there is much resemblance between *Phoronis* and *Terebratulina*, but in the latter animal the mesocœlomic and meta-cœlomic cavities are entirely absent.

¹ Since the appearance of Ideka's (1901) work this statement is no longer true. Ideka has given by all odds the most complete account of the embryology of *Phoronis* yet published. (See postscript, p. 70.)

Very little is certainly known of the formation of the mesoderm and coelom among the Bryozoa. In the Ectoprocta the larval form is usually solid, the coelom and enteron having undergone extensive if not complete degeneration, while in those forms in which the coelom is still preserved its method of origin is highly peculiar. For example, in the Phylactolæmata the central cavity of the embryo is generally considered to be the coelom, although at the stage at which it appears there is neither endoderm nor enteric cavity in the embryo (see Korschelt and Heider's Text-Book).

Among the Endoprocta the mesoderm arises in *Pedicellina*, according to Hatschek, from two pole cells which appear at the posterior edge of the blastopore; these cells by repeated divisions give rise to two short mesoderm bands, and from these bands mesoderm cells arise which fill the space between the ectoderm and the endoderm. It appears therefore that no direct comparison can be made between *Terebratulina* and the Bryozoa in the matter of the formation of mesoderm and coelom.

3. *Orientation of Embryo and Larva.*—As has been pointed out already the relation of the chief axis of the gastrula to the chief axis of the larva is the same as is found in all Heteraxonia (Hatschek) or Hypogastric forms (Goette). The animal pole of the egg and the apical pole of the gastrula become the cephalic pole (*Hirnfeld*) of the larva, while the blastopore comes to lie on the ventral side. Such a relation of the embryonic and larval or adult axes is of very general occurrence, being found at least in all Trochozoa (Hatschek). Moreover in having a blastopore which becomes narrow from side to side and then closes from behind forward, and also in the formation of the stomodæum at the place where the blastopore closed, *Terebratulina* agrees with a large number of bilateral animals belonging to widely different phyla. These characters are so general, therefore, as to be of little value in determining the affinities of the brachiopods. Regarding the apical sense plate as anterior and the suboesophageal sense plate as ventral in position, it follows that the peduncle is posterior and the mantle folds dorsal and ventral; consequently even after the metamorphosis the peduncle is posterior, and the valves which are formed by the mantle folds are dorsal and ventral, while the opening of the valves is anterior. This orientation is the commonly accepted one and is directly opposed to Caldwell's ('82) remarkable views, according to which both valves and the peduncle are ventral in position.

4. *General Morphology of Larva.*—The resemblances between the early embryos of *Terebratulina* and those of other metazoa are so general in character that they afford little assistance in determining the affinities of the brachiopods. We must therefore rely largely upon the structure of the larva and of the adult for the solution of this problem.

(a) *Comparison with Trochophore.*

Among the chief characteristics of the trochophore larva, as enumerated by Hatschek ('88, p. 307), are the following :

- I. (1) Bilateral symmetry, (2) mouth on ventral side, (3) anus near posterior end, (4) shape ovoid.
- II. (5) Apical tuft of cilia, (6) preoral ciliated band (Trochus), (7) postoral ciliated band (Cingulum), (8) adoral ciliated zone, (9) ventral ciliated furrow between mouth and anus, (10) small cilia over general surface of larva.
- III. (11) Epithelial nervous system, (12) apical plate (*Schietelplatte*), ganglion and sense organs, (13) œsophageal nerves and buccal (ventral) ganglion, (14) ventral (and sometimes dorsal) longitudinal nerves.
- IV. (15) Alimentary canal (œsophagus, stomach and intestine) horseshoe-shaped and ciliated throughout, (16) stomach retort-shaped, (17) intestine reaches to posterior end of body.
- V. (18) Mesoderm partly mesenchymatous, partly epithelial, (19) mesenchyme gives rise to branched connective tissue cells and thread-like or branched muscle cells, (20) ventral and dorsal longitudinal muscle pairs, (21) preoral and postoral ring muscles, (22) dilators and constrictors of œsophagus and intestine, (23) mesothelium gives rise to the paired protonephridium, which is a longitudinal ciliated tube closed at the anterior end by terminal cells, and opening posteriorly on the ventral side in front of the anus, (24) paired coelomic sacs at the posterior end.

Of these characteristics, numbers 5, 6, 7, 8, 11, 12, 13, 15, 16, 17 and 23 are undoubtedly the most important, and all of these except the last are found also in brachiopod larvæ. All investigators of the embryology of brachiopods have described the apical tuft of cilia (5); the preoral ciliated band (6) is probably

represented in the brachiopod larva by the circle of longer cilia found at the base of the preoral lobe (see Kowalevsky's figures of *Argiope* larvæ); the postoral ciliated band (7) is probably represented by the mantle, which attains a much greater development in the brachiopod larva than in the ordinary trochophore; the adoral ciliated furrow (8) is represented by the anterior mantle furrow; the fact that adult brachiopods have an epithelial nervous system (11) has long been known, and I have observed the beginnings of such a nervous system in the larva of *Terebratulina*; I have also observed (p. 55) the apical plate and ganglion (12) and the ventral plate and ganglion (13) in *Terebratulina*; only the beginnings of the œsophageal invagination are shown in the oldest larva which I have studied, but it is evident from its position that after it joins the stomach the alimentary canal will be horseshoe-shaped (15); the stomach in *Terebratulina* larvæ is retort-shaped (16) and the intestine reaches to the posterior end of the larva (17).

In addition to these more important characteristics the larvæ of *Cistella*, *Thecidium* or *Terebratulina* agree with the trochophore in the possession of the following characteristics: Bilateral symmetry (1), blastopore and *anlage* of mouth on ventral side (2), ventral blastopore groove (9) and general ciliation of body (10), mesoderm partly mesenchymatous, partly epithelial (18); finally ventral and dorsal longitudinal muscles (20) are present in the peduncle of *Cistella*. These brachiopod larvæ also agree with many chætopod larvæ in the possession of ectodermal seta sacs and provisional setæ.

The points in which the larvæ of testicardinate brachiopods differ most from the trochophore are in the absence of mouth and anus and the lack of a protonephridium. In the Ecardines however both mouth and anus are present during larval life, and in all brachiopods a single pair of nephridia appears after the larval period. The absence of these larval structures therefore indicates a retardation or less perfect development of the larval brachiopod as compared with the typical trochophore. I believe therefore that the brachiopod larva belongs unquestionably to the trochophore type.

(b) *Comparison with Actinotrocha.*

The larva of *Phoronis*, while showing many peculiarities, bears a most decided resemblance to the trochophore. Among its principal characteristics may be enumerated the following:

- I. (1) There are three sections of the body: (a) the preoral lobe, (b) the postoral section (collar) which carries tentacles, and (c) the posterior or anal section (trunk); (2) the preoral lobe probably represents the umbrella of the trochophore; (3) the cilia at its margin probably correspond to the preoral ciliated band (Trochus), while (4) the postoral ciliated zone (collar) which carries the tentacles probably corresponds to the postoral band (Cingulum) of the trochophore; (5) this postoral ciliated zone (Cingulum) runs obliquely around the body, being further posterior on the ventral than on the dorsal side; (6) tentacles appear near the ventral midline and fresh pairs are added dorsally.
- II. (7) There is an epithelial nervous system, (8) an apical plate, ganglion and (in some species) eye spots, and (9) an œsophageal commissure.
- III. (10) The cœlom is composed of an anterior unpaired cavity and two pairs of cavities posterior to this (Masterman);¹ (11) the anterior cœlom sac arises as an enterocœl, the posterior paired ones as schizocœls; (12) there is one pair of protonephridia, which end blindly internally in connection with excretory cells.
- IV. (13) There is a ventral invagination posterior to the zone of tentacles and a peculiar metamorphosis by the evagination of this invagination; (14) during metamorphosis the tentacles turn forward, and (15) the anus comes to lie on the dorsal side of the mouth, the intestine thus forming a loop.

Comparing now the larvæ of brachiopods with the Actinotrocha we find that, in addition to the general resemblances to the trochophore which both show, there are the following special resemblances between the two: (1) In both brachiopods and Actinotrocha the postoral ciliated zone (Cingulum) is greatly enlarged and runs obliquely around the body, being farther posterior on the ventral than on the dorsal side. (2) In both cases this forms the mantle or lophophore, though the tentacles or cirri which are borne upon it appear much earlier in Actinotrocha than in the brachiopod larva. (3) Brooks has shown that in *Lingula* the ventral pair of

See postscript, p. 70.

tentacles appears first and that successive pairs of tentacles are added dorsally, exactly as in *Actinotrocha*. (4) In the metamorphosis the mantle (lophophore) is turned forward over the preoral lobe in exactly the same way in both cases. These are extremely important resemblances, and in themselves lend support to the view that *Phoronis* and the Brachiopoda are closely related.¹

On the other hand, according to Masterman's ('97 and 1900) recent work on *Actinotrocha*, there are certain important respects in which *Actinotrocha* differs decidedly from the brachiopod larva: (1) The coelom consists of an anterior unpaired cavity and of two pairs of cavities, one of which lies in the lophophore and the other in the trunk region. The anterior unpaired cavity somewhat resembles in position and method of origin the anterior portion of the enterocoel of *Terebratulina*, but the lophophoral and trunk cavities of *Actinotrocha* differ from the mantle and peduncular coelom of *Terebratulina* in that the latter are a part of the enterocoel and are never completely separated from one another, whereas in *Actinotrocha* they arise as schizocoels and are always separate. (2) *Actinotrocha* also has rudiments, at least of a second pair of nephridia. (3) It also has two endodermal outgrowths from the anterior portion of the enteron, which are composed of large vacuolated cells, and are homologized by Masterman with the notochord of the Hemichorda.²

I have had no opportunity of studying the later stages in the development of the brachiopod, in which alone the two last-mentioned structures might be looked for, and cannot therefore determine whether there are real differences between the brachiopod and *Phoronis* in these respects. With regard to the differences shown by the coelom, one must bear in mind the fact that in the brachiopod larva the coelom almost entirely disappears, except in the mantle, and a segmentation of the coelom in later stages could not therefore be observed, even if it had at one time existed in the ancestors of the brachiopods. There can be no doubt however that in *Terebratulina* the entire coelom arises from a single enterocoel, in which respect there is a decided difference between the brachiopod and *Phoronis*. The resemblances mentioned above

¹ The presence of "plasmic corpuscles" (Ideka, 1901) in the blastocoel of both forms is another interesting resemblance (see p. 45).

² See postscript, p. 70.

however are so important and extend to such details that I am inclined to accept the view that *Phoronis* and the Brachiopoda are related, and to look to future work on the development of both of these groups to harmonize the apparent differences between them.

(c) *Comparison with Larval Polyzoa.*

Brooks in particular has emphasized the resemblance between the larvæ of Polyzoa and Brachiopoda, basing this comparison, however, rather upon the external characters in which both resemble the trochophore than upon a detailed comparison of internal structure.

Ectoprocta.—It is extremely difficult to compare larval brachiopods with larval ectoprocts, owing to the great variety of forms presented by the latter, their many secondary characters, and the conflicting accounts of their structures and homologies which have been given by various authors. There is some reason for believing however that the ectoproct larva belongs to the trochophore type, and that the following parts of the two may be homologous: (1) The retractile disk may correspond (at least in part) to the apical plate, (2) the corona in part to the trochus, (3) the sucker to the trunk of the trochophore, or to the ventral evagination of Actinotrocha. Furthermore one may trace a certain resemblance between the invaginated sucker of *Bugula* and *Lepralia* and the peduncle and mantle of *Terebratulina*. In both cases attachment takes place by the peduncle, while the covering folds (mantle in the case of brachiopods) are turned forward as the peduncle is protruded. However the degeneration and modification of structures, both in the larval stages and in the metamorphosis, are so extreme that any attempt at the present time to trace homologies between larval Ectoprocta and other forms must be accompanied by a lively imagination and a ready facility in guessing.

There is good evidence in the degeneration of the intestine and coelom of the ectoproct larva, and in the general degeneration which accompanies its metamorphosis, that we are dealing with a highly modified type of development, which is little likely to throw light upon the affinities of the Polyzoa. However the resemblances between the adult Polyzoa and *Phoronis* and the Brachiopoda is such as to warrant the conclusion that these groups are at least remotely related to one another.

Entoprocta.—Among larval entoprocts there are few, if any, undoubted homologies with either the trochophore, the actinotroch,

or the brachiopod larva. It is possible that the ciliated disk of *Pedicellina* and *Loxosoma* is homologous with the retractile disk of the ectoproct larva and with the apical plate of the trochophore, and that the margin of the vestibule (ciliated ring) in the former corresponds to the trochus of the latter, but these possible homologies are too hypothetical to be affirmed with any degree of assurance.

5. *Conclusions.*—Neglecting the older views as to the affinities of the brachiopods with lamellibranchiate Mollusca, which were founded merely upon superficial resemblances, we find that within recent times the brachiopods have been associated, at different times and by different authors, with Chætopoda, Polyzoa, Chæ-tognatha and Phoronis.

Both Morse ('73²) and Kowalevsky ('74) independently reached the conclusion that the brachiopods are chætopod annelids. Morse says in summing up his work on the subject ('73², p. 57): "We must regard the brachiopods as *ancient cephalized chætopods*, while *Serpula*, *Amphitrite*, *Sabella*, *Protula* and others may be regarded as *modern* (later) *cephalized chætopods*"; and Kowalevsky ('74) maintained that the brachiopods ought to be considered simply as an order of the annelids, which present at least as many resemblances to the chætopods as do the leeches.

Morse has enumerated twenty-four characteristics in which brachiopods resemble more or less closely Vermes, sedentary annelids and Gephyreans. Kowalevsky also names a considerable number of points in which brachiopods resemble chætopods. Some of these features are not actually characteristic of the brachiopods, as, for example, the segmentation of the larva; others are of such a general character as to apply to almost all Bilateralia, as Brooks has shown, while still others represent real resemblances between the brachiopod larva and the trochophore. The trochophore larva however is of such wide occurrence among bilateral animals, that the mere classification of the brachiopods among the Trochozoa throws no light upon the nearer affinities of this group.

Huxley, Lankester, Claus and others have regarded the brachiopods as more or less closely related to the Polyzoa, and Brooks in particular has held that the two groups belong to the same phylum and class. "The organization of the *Lingula* larva," he says, "shows that it is not merely like a Polyzoan, but that it actually is one; as much so as the hydra stage of an Hydro-Medusa is a

Hydra, or the tailed larva of Botryllus is an Appendicularia, and more so than a tadpole is an urodelan Batrachian." This close relationship he bases largely upon the external resemblances between the larvæ of *Thecidium* and various Polyzoan larvæ. It seems to me that some of these resemblances are real homologies, but on the other hand the differences between these larvæ, as well as between the adults of these two groups, are so great that it would be inadvisable to place them together in the same class; though I believe they should be placed in the same phylum. Moreover it seems to me that Brooks' view, that the Polyzoa are the ancestral form of which the Brachiopoda are a specialization, is just the reverse of the real relationship; larval as well as adult Brachiopoda show less specialization and certainly less degeneration than the Polyzoa.

The resemblances of the brachiopod larva to the Molluscan veliger, upon which Brooks lays emphasis, are in the main the same as the resemblances to the trochophore, the veliger and trochophore belonging to the same type of larva.

The idea that the brachiopods are related to the chætognaths, which was suggested by Bütschli and Hertwig ('80) and maintained by van Bemmelen ('83), has little more in its favor than the supposed resemblance in the method of formation of the coelom and in certain histological details.

So far as the formation of the coelom is concerned, I have already pointed out the fact that in *Terebratulina* it forms in a very different manner from what obtains in *Sagitta*, and as for the histological resemblances they are by no means confined to the two groups in question. On the other hand there are so many important differences between the two groups, both in their embryology and in their adult structure, that one could as well maintain the affinity of the Brachiopoda with Echinodermata, Enteropneusta or Chordata, as with Chætognatha.

Caldwell ('82) first pointed out in detail the resemblances between *Phoronis* and the Brachiopoda. In this paper he has urged "an entirely new view of the homologies of the body surfaces in Brachiopoda." He regards the Brachiopoda as fixed by their ventral surface, and both valves of the shell as ventral in position, the peduncle of the brachiopod corresponding to the ventral invagination of Actinotrocha. While there are some facts which may be urged in favor of this view there are many which may be used

against it. The fact that in both *Phoronis* and *Lingula* the intestine forms a loop, the anus opening near the mouth, and that fixation takes place by the posterior extremity, has led to Caldwell's view as to the homologies of the body surfaces in the brachiopods. On the other hand the ventral mantle fold of *Terebratulina* forms directly across the region where the blastopore lips fused and immediately posterior to the place where the blastopore remnant closed and where the mouth later appears. Upon the anterior face of this fold the suboesophageal sense plate and ganglion appear; there can be no doubt therefore that this fold is ventral in position. The dorsal mantle fold appears at a very early stage (Figs. 16 and 20) on the apical side of the gastrula and just posterior to the chief gastrula axis; it is impossible therefore that it should be considered as ventral in position. *Furthermore the mantle folds of the brachiopod correspond to the zone which bears the tentacles in Actinotrocha* (collar, Masterman) *and not to the margins of the ventral invagination*; and since the mantle folds surround the body posterior to the mouth, both of them cannot be ventral in position. Whether the peduncle is ventral or not cannot perhaps be determined with certainty until we know the embryology of a brachiopod in which the anus and terminal portion of the intestine are present. In *Lingula*, as is well known, the anus opens near the mouth and on the left side; in *Crania* it is terminal in position, and the embryology of either of these forms should throw light on this question as to the morphological position and homologies of the peduncle. Brooks' work on *Lingula* deals only with stages in which the anus and the intestinal loop are already present, and one cannot therefore tell at what point relative to the blastopore the anus appears and how the loop is formed. It is certain however that the ventral invagination and remarkable metamorphosis of *Actinotrocha* are coenogenetic rather than phylogenetic characteristics, and that parallel phenomena need not be expected in other groups of animals. Furthermore it is certain that the peduncle in *Terebratulina* is derived from that portion of the gastrula which is posterior to the blastopore; I do not see therefore how it can be regarded as ventral in position. But however this problem of the relation of the peduncle of the brachiopod and the ventral invagination of *Actinotrocha* may be decided by future work, it seems to me that the affinities of *Phoronis* and Brachiopoda are well established. I agree therefore in the main with the views of Caldwell, Lang and Blochman, and

more particularly with the position of Heider, as to the affinities of the brachiopods. The relationship between Phoronis, Bryozoa and Brachiopoda seems to me sufficiently close to justify the placing of them in the same phylum, though not in the same class, as Lang has done.

POSTSCRIPT.

Since this paper was written I have seen Ideka's (1901) very important contribution on the "Development, Structure and Metamorphosis of Actinotrocha." Ideka's work is in all respects the most thorough and extensive which has yet been done on the development of Actinotrocha, and in many very important points he differs decidedly from Masterman. Some of the differences between Actinotrocha and the brachiopod larva, which are pointed out on p. 65, disappear in the light of this work. For example, Ideka finds that there is but one complete septum in the body, that between the collar and the trunk, while the cavities of the preoral lobe and collar are in communication through a very incomplete septum. Furthermore Ideka finds no trace of a second pair of nephridia or of a "proboscis pore," such as Masterman described, while the two "chorda" diverticula of Masterman (Diplochorda) are represented by a single unpaired diverticulum in the Japanese species. Whether this is a glandular or skeletal structure is left an open question.

With the exception then of the single septum between the collar and the trunk regions there are no important differences between Actinotrocha and the brachiopod larva. This septum occupies a position in Actinotrocha corresponding to the posterior mantle furrow of the brachiopod larva, and it would be interesting to know whether, in stages of the brachiopod larva later than those which I have studied, any trace of a septum can be found in this position.

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REFERENCE LETTERS.

- Bc*, Blastocœl.
- Bf*, Blastopore groove.
- Bp*, Blastopore.
- Br*, Blastopore remnant.
- C*, Cœlom.
- Ce*, Enterocœl.
- Cc*, Cephalic Cœlom.
- Cm*, Mantle Cœlom.
- Cp*, Peduncular Cœlom.
- Ccm*, Cephalic and Mantle Cœlom.
- Cmd*, Dorsal extension of Mantle Cœlom.
- Cmv*, Ventral extension of Mantle Cœlom.
- CG*, Apical Sense Plate and Cerebral Ganglion.
- D*, Dorsal.
- DA*, Dorsal-Anterior.
- E*, Enteron.
- Em*, Egg Membrane (ectoplasmic layer).
- Fa*, Anterior Mantle Furrow.
- Fp*, Posterior Mantle Furrow.
- Gc*, Gastrocœl.
- M*, Mantle.
- Md*, Dorsal Mantle Fold.
- Mv*, Ventral Mantle Fold.
- mc*, Mesenchyme.
- O*, Point where blastopore closed and œsophageal invagination appears.
- P*, Peduncle.
- Pb*, Polar Bodies.
- PC*, Peduncular Chamber.
- Pg*, Dark Staining Granules.
- SG*, Ventral Sense Plate and Sub-œsophageal Ganglion.
- SS*, Setæ Sacs.
- V*, Ventral.
- VP*, Ventral-Posterior.

DESCRIPTION OF FIGURES.

All the figures illustrating this paper were drawn with Camera Lucida at the stage level under a Zeiss Apochromat. Homog. Immers. Obj. 3mm. Comps. Occ.

4. In the process of reproduction they have been reduced about one-third.

PLATE I.

- Fig. 1. One-cell stage; polar body in process of being formed; egg elliptical; ectoplasmic layer surrounds egg and polar body.
Fig. 2. Two-cell stage; one cell larger than the other; three polar bodies present.
Fig. 3. Transitional stage between two-cell and four-cell stages; showing overlapping of certain cells and "spiral" character of cleavage.
Fig. 4. Four-cell stage, two cells (at right) larger than the other two; protoplasmic areas surrounding nuclei shown; two polar bodies lie in the polar furrow.
Fig. 5. Eight-cell stage, apical view; three polar bodies at animal pole.
Fig. 6. Eight-cell stage, side view; one polar body at animal pole.

PLATE II.

- Fig. 7. Eight-cell stage, apical view; each cell indented at periphery; polar furrows at right angles to each other at opposite poles.
Fig. 8. Seven-cell stage; irregular cleavage; animal pole indicated by three polar bodies.
Fig. 9. Sixteen-cell-stage, apical view; two polar bodies at animal pole.
Fig. 10. Sixteen-cell stage, optical section, showing blastocoel, ectoplasmic layer (*Em*) and polar body or yolk spherule between two of the cells.
Fig. 11. Twenty-cell stage; some of the cells elongated and probably dividing yolk spherules within blastocoel.
Fig. 12. About forty-eight-cell stage; egg flattened by pressure and the blastomeres partially separated.

PLATE III.

- Fig. 13. Early invagination stage, optical section.
Fig. 14. Gastrulation completed; blastocoel obliterated; gastrocoel partially divided into enteron (*E*) and enterocoel (*Ce*).
Fig. 15. Optical section of older embryo, viewed from posterior; enteron still further constricted from enterocoel.
Fig. 16. Optical section of embryo of same stage as preceding, lateral view, showing anterior extension of enterocoel and partition wall growing down on anterior side between enteron and enterocoel.

- Fig. 17. Oral view of embryo, showing elongated blastopore opening at its anterior end into the enterocœl and enteron; the enterocœl but little larger than the enteron.
- Fig. 18. Antero-ventral view of an embryo of about the same stage as the preceding.

PLATE IV.

- Fig. 19. Optical section of older embryo, viewed from posterior; showing the enteron separated from the enterocœl.
- Fig. 20. Optical section of an embryo of same stage as preceding, lateral view; showing the enteron almost entirely separated from the enterocœl.
- Fig. 21. Oral view of an embryo of about the same stage as the preceding; the blastopore narrower than in preceding stages; the enteron completely cut off from the enterocœl except in the region of the blastopore; mesenchyme cells (*mc*) line the anterior part of the enterocœl.
- Fig. 22. Oral view of an older embryo in which the blastopore has closed to a narrow groove except for a small opening near its anterior end; mesenchyme cells are abundant in the anterior and posterior parts of the enterocœl; mantle folds show at the sides of the embryo.
- Fig. 23. Aboral view of an embryo of the same stage as the preceding, showing dorsal mantle fold (*M*).
- Fig. 24. Optical longitudinal section of an embryo in which the blastopore has completely closed, leaving however on the ventral surface the blastopore remnant (*Br*) and groove; the dorsal mantle fold (*Md*) and furrow are shown on the dorsal side; the enteron still communicates with the enterocœl at its posterior end.

PLATE V.

- Fig. 25. Dorsal view of a larva in which cephalic, mantle and peduncular regions are well defined.
- Fig. 26. Ventral view of an older larva, showing the ventral mantle folds meeting in the region of the blastopore groove (*Bf*); the blastopore remnant (*Br*) lies in a notch on the anterior side of the mantle fold.
- Fig. 27. Dorsal view of a slightly older larva, showing the increased prominence of the mantle and the lobulation of the cœlom.
- Fig. 28. Optical longitudinal section of a larva of the same stage as the preceding, showing the dorsal and ventral mantle folds (*Md* and *Mv*); apical sense plate and ganglion; enteron and cœlom.
- Fig. 29. Ventral view of an older larva, showing the ventral mantle folds fused in the midline; the anterior and posterior mantle furrows are shown as shaded lines; in the anterior mantle furrow the place at which the blastopore remnant disappeared and where the cesophageal invagination will occur is marked (*O*); the apical and ventral sense plates (*CG* and *SG*).

- Fig. 30. Dorsal view of a larva of the same stage as the preceding, showing the dorsal mantle fold (*Md*); the anterior and posterior mantle furrows; the union between the two halves of the peduncular coelom.

PLATE VI.

- Fig. 31. Lateral view of a larva of the same stage as the preceding, showing anterior and posterior mantle folds (*Fa* and *Fp*), apical and ventral sense plates (*CG* and *SG*), enteron and coelom.
- Fig. 32. Dorsal view of older larva, showing increased prominence of mantle and deep constriction of anterior mantle furrow.
- Fig. 33. Dorsal view of an older larva, showing the mantle in process of growing back over the peduncle; the coelom is almost entirely confined to the mantle.
- Fig. 34. Dorsal view of one of the oldest free-swimming larvæ; the mantle has almost entirely covered the peduncle.
- Fig. 35. Lateral view of a larva of the same stage as the preceding, showing apical and ventral sense plates (*CG* and *SG*), dorso-ventral extension of enteron and greater width of mantle chamber on dorsal side.
- Fig. 36. Optical section in longitudinal frontal plane of a larva of the same stage as the preceding, showing apical sense plate and cerebral ganglion; mantle chamber and setæ sacs; cephalic, peduncular and mantle coelom (*Cc*, *Cp*, *Cm*).

PLATE VII.

- Fig. 37. Section of an embryo of the stage shown in Fig. 13, showing dark staining granules in the outer ends of the cells and yolk spherules in the blastocoel.
- Fig. 38. Section of an embryo of the stage shown in Fig. 14.
- Figs. 39-42. Four transverse sections of an embryo of the stage shown in Fig. 20; Fig. 39 being the most posterior and Fig. 42 the most anterior section drawn.
- Figs. 42*a* and 42*b*. Longitudinal sections through an embryo of about the same stage as is shown in Figs. 39-42, showing the formation of the septum which separates the enteron from the enterocoel.

PLATE VIII.

- Figs. 43-47. Five transverse sections of a larva of the stage shown in Fig. 24; Fig. 43 being the most anterior and Fig. 47 the most posterior section drawn.
- Figs. 48-52. Five transverse sections of a larva of the stage shown in Fig. 29; Fig. 48 being the most anterior and Fig. 52 the most posterior section drawn.

PLATE IX.

- Figs. 53-55. Three oblique sections from the dorsal anterior (*DA*) to the ventral posterior (*VP*) region of a larva of the stage shown in Fig. 31 (the sections are nearly in the plane of the reference line from *E* in Fig. 31).
- Figs. 56, 57. Two longitudinal frontal sections of a larva of the same stage as the preceding, Fig. 56 being ventral to Fig. 57.
- Fig. 58. Longitudinal sagittal section of a larva of the same stage as the preceding; the section passes through both the apical and the ventral sense plates (*CG* and *SG*).

PLATE X.

- Figs. 59-64. Six transverse sections of a larva of the stage shown in Figs. 34-36; Fig. 59 being the most anterior and Fig. 64 the most posterior section drawn. Fig. 59 passes through the cephalic region; Fig. 60 lies just behind the anterior mantle furrow; Figs. 61-64 are through the mantle and peduncle.